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## DISCOVERY OF THE FEMALE *PLUMARIUS* (HYMENOPTERA, PLUMARIIDAE)<sup>1</sup>

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The family Plumariidae has long been a puzzle to hymenopterists. It is represented by two poorly known genera: *Plumarius*, which ranges throughout arid and semiarid regions from Ecuador to Chile and Argentina, and *Myrmecopterina*, known from semiarid situations in South Africa. The two genera are very similar; both are of generally pale coloration and possess large eyes and ocelli, not unlike other nocturnal Aculeata such as certain Mutilidae and Tiphidae. Both genera have been known for many years from males only, and nothing whatever is known of their biology. They are commonly placed in the superfamily Scolioidea, although their strange antennae and wings, unusual development of the front of the head, long legs, lack of constriction between the first two metasomal segments, and other unusual features leave one wondering if this is, in fact, the correct taxonomic assignment for this family.

Many years ago my former professor, J. C. Bradley (1921a), remarked regarding *Plumarius* that "any one who will discover and make known the female and her habits will cover himself with well merited distinction . . . The female will undoubtedly yield important evidence of the correct systematic position for the genus." The distinction of discovery belongs to Drs. E. S. Ross and E. I. Schlinger, who collected two females in Peru and sent them to me as Bethyridae. After much study, I am convinced they can be nothing other than females of the genus *Plumarius*. The distinction of elucidating their habits remains to be claimed.

These two females were collected 22 miles north of Pativilca, in Lima Province, Peru, on January 15, 1955, at 150 meters elevation.

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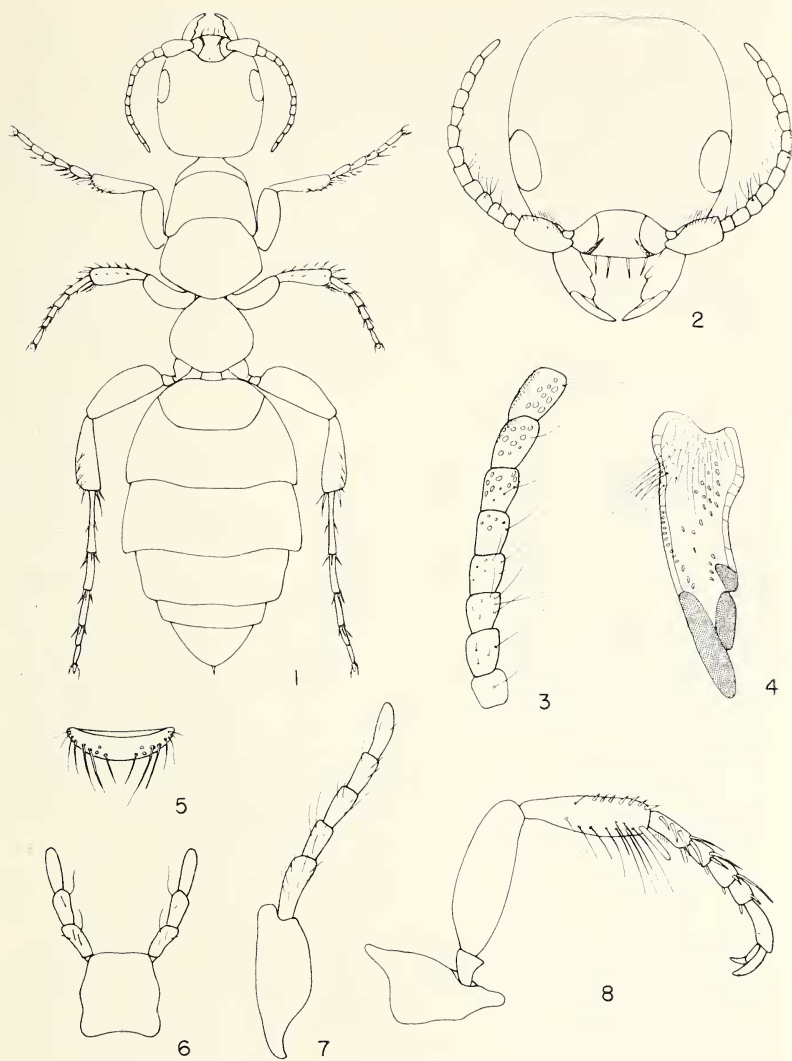
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Dr. E. S. Ross writes that these specimens were collected in the daytime during a search for Embioptera, probably "under stones on sandy silt". "The locality was extreme desert typical of coastal Peru. It must have shown some effects of coastal fog, such as lichens on rocks, else we wouldn't have stopped for embiids" (E. S. Ross, *in litt.*). Dr. E. I. Schlinger recalls this as a "loma zone surrounded by arid to semi-arid vegetation". He collected spiders under rocks and believes the wasps may have been collected there, too. Since these females have all the features of hypogaecic Hymenoptera, their occurrence under rocks seems logical enough.

Ross and Schlinger collected many male *Plumarius* in Peru (though none at this locality) and Dr. Marius Wasbauer has been studying these in a preliminary way. He writes that there appear to be three species in Peru and Ecuador. Since *Plumarius* is completely unworked taxonomically, I shall refrain from placing a specific name on the females. The specimens have been returned to the California Academy of Sciences, where they await inclusion in a much-needed revision of this genus (hundreds of males have now accumulated in museums).

I shall present first a detailed description of these females, then a few notes on male structure, and finally a discussion of the probable relationships of the Plumariidae. Since both females are somewhat imperfect, my description is a composite from the two specimens, parts of one of which have been mounted on a slide. The two specimens are virtually identical in size and structure.

*Description of the female Plumarius.* — Length about 5 mm; body somewhat depressed, wings and tegulae completely absent (Fig. 1); body light castaneous, shining, the appendages testaceous. Head strongly depressed, very thin, prognathous; eyes of moderate size, not protruding from surface of head, each containing approximately 150 facets; ocelli absent (Fig. 2). Occipital carina closely surrounding foramen, complete but not at all visible in frontal view; under surface of head with mouth-parts far removed from occipital foramen, the space filled by a broad genal bridge, the midline narrowly depressed but not really sulcate; hypostomal sulcus closely paralleling the margin of the broad proboscoidal fossa. Labium simple, palpi with three subequal segments (Fig. 6); maxillae small, closely associated with labium, bearing fairly long, 5-segmented palpi (Fig. 7); mandibles large, strongly tapered toward the apex, bearing three large apical teeth, each of them (but especially the large apical tooth) marked by a thick, horny plate; mandibles with many small sensilla and with numerous setae arising near the base (Fig.



Figures 1—8. Structure of female *Plumarius*, from locality 22 miles N of Pativilca, Peru. Fig. 1. Dorsal view of body. Fig. 2. Frontal view of head. Fig. 3. Detail of antennal segments 2-9. Fig. 4. Mandible. Fig. 5. Labrum. Fig. 6. Labium. Fig. 7. Maxilla. Fig. 8. Front leg.

4); labrum concealed by the clypeus except for some of its long apical setae, when dissected away found to be very short, semicircular (Fig. 5). Clypeus broad, weakly rounded apically, its median area rather flat, but the sides deeply hollowed out for the reception of the scape; apical margin, opposite the antennal insertions, with a pair of tufts of matted setae (Fig. 2); front weakly, evenly convex, strongly shining, without punctures or setae, distance between eyes measuring  $2.6 \times$  eye height; distance from eye tops to vertex crest much exceeding eye height, the vertex very broadly rounded, slightly concave at the midline, the crest rather sharp. Antennae with 13 well-defined segments, arising from simple orbits; middle segments weakly serrate; segments 2-9 each with one or more fairly prominent setae, segments 6-13 with a variety of prominent sensory pores and spicules (Figs. 2, 3).

Thorax and propodeum also strongly polished and virtually without surface sculpturing, with a few pale setae arising from constricted portions such as the neck region, the thoracic-propodeal junction, and the propodeal-metasomal junction; greatest width of thorax (across the mesothorax) subequal to width of head; pronotum fairly long, its posterior margin arcuate, with weakly developed, slightly rounded posterior lobes; proepisterna unusually large and convex, roughened ventrally with small, wart-like protuberances, the midventral line of the prothorax indistinctly sulcate; prosternum small, poorly differentiated; base of front coxa with a partially separated sclerite which may represent the proepimeron (Fig. 11). Mesothorax broad, smooth, with no separation whatever into scutum, scutellum, or pleura; metathorax apparently absent, the hind legs appearing to rise from the propodeum close to the articulation of the metasoma; propodeum narrowly connected to thorax, depressed, its contours very smooth. Coxae large, conical, all three pairs contiguous medially and also capable of overlapping when the legs are pressed against the body; front coxae terminating in a flattened process which extends beyond the origin of the trochanters; hind femora incrassate, front femora more weakly so; all tibiae spinose as figured; tibial spurs 1-2-2, the spur of the front tibia not forming a well defined antennal cleaner; front tarsus with a pecten of short, stout spines (Fig. 8), other tarsi very slender, rather bristly at the joints; claws simple, arolia fairly large.

Metasoma broad, attached to propodeum by a petiole which is no longer than broad; first tergite short, its posterior margin arched; first sternite short, broadened slightly behind the petiole but apparently broadly overlapped by the large second sternite. Sixth

(apical) segment rather broad, simple, non-setose, giving rise to an apparently rather short sting.

*Comments on characters of male Plumarius.*—Evidence that the females just described represent the opposite sex of nocturnal males of the genus *Plumarius* may be summarized as follows: (1) both males and females are of generally light brown coloration; (2) Peruvian males I have seen are of about the size one would predict for males of the wasp described above; (3) both sexes have erect setae on the antennae, although these are much more abundant in the male; (4) the labium is very similar, the labial palpi 3-segmented in both sexes (much as in Fig. 6); (5) in both sexes the mandibles are tridentate, the teeth thickened and heavy, and the mandibles have numerous setae and sensilla; (6) the labrum of the male is small, bristly, and mostly or wholly concealed by the clypeus, though in general more narrow than in the female; (7) in both sexes the prosternum is very large, and there is a partially differentiated sclerite just in front of the anterior coxae which probably represents the proepimeron (Figs. 11 and 12); (8) all coxae are subconical, and the members of each pair are contiguous or nearly so; (9) the mesopleura are strongly swollen; (10) there is no constriction between the first two metasomal sternites.

In spite of these many similarities, the males are radically dissimilar to the females in many features: they have large eyes and ocelli, the wings are fully developed, and the thorax is without the many reductions associated with flightlessness; the maxillary palpi are much longer and have six segments rather than five; the face and clypeus are unusually elongate; the abdomen is sessile; and of course there are the usual differences in the form of the abdomen and in the genitalia. On the whole the sexual dimorphism is no greater than one has learned to expect in certain Tiphidae (Brachycistidinae, Thynninae) or Bethylidae (Pristocerinae).

In the effort to determine the correct systematic position of the Plumariidae, it seemed desirable to make a preliminary study of the terminal segments of the male abdomen, since the family was omitted by Snodgrass (1941) and others who have studied the male genitalia of Hymenoptera. The apical tergite (Fig. 14) is of generalized structure and bears pygostyles much longer than any known in the Bethylidae, though not dissimilar to those of certain Mutillidae and Formicidae (Snodgrass, 1941, plates 13, 14). The apical sternite (Fig. 13) is a simple, tongue-shaped structure similar to that of certain Formicidae or Bethylidae, and quite unlike the pseudosting of most Scoliidea. The genitalia (Fig. 15) are of basically simple

structure. The small basal ring and form of the aedoeagus and volsellar structures are all suggestive of the Bethyloidea; however, there is no clear separation of the parameres from their basal plates, a feature more characteristic of the Scolioidea and certain Formicidae. All of this is of some academic interest, but at the same time one is left with the feeling that although the terminalia of *Plumarius* do not quite resemble those of known Bethyloidea, Scolioidea, or Formicoidea, in fact there seem to be no well defined superfamilial characters in the genitalia. One can at least say that there are no noteworthy reductions or specializations in the terminalia of *Plumarius*.

*The systematic position of the Plumariidae.*—It is sometimes stated that the major feature of the Bethyloidea is the lack of sexual dimorphism in antennal segmentation. If this is true, these wasps belong in the Bethyloidea. Other bethyloid features include the head shape of the female, segmentation of the labial palpi, lack of constriction between the first two metasomal segments, and the genitalic features mentioned above. However, the broad, well-veined hind wings, with distinct closed cells, tend to eliminate the group from the Bethyloidea, as do the spinose front and hind legs. The Bethyloidea must, of course, have evolved from an ancestor having a more complete venation, just as the Scolioidea undoubtedly evolved from an ancestor lacking sexual dimorphism in the antennae. I suggest that *Plumarius* is a relic of an ancient stock, one portion of which gave rise to the Bethyloidea, another to the Scolioidea and higher wasps. This ancient stock has apparently managed to survive by becoming adapted to severe desert conditions in South America and South Africa, the males being nocturnal, the females hypogaecic.

It should be noted that Sharov (1957) has described and figured the wing of a supposed wasp from the Cretaceous of Siberia, *Cretavus sibiricus* (Fig. 10), pointing out the resemblance of the wing to that of *Plumarius* (Fig. 9). Although some differences are obvious, particularly in the shape of the stigma and marginal cell, there are indeed some striking similarities, particularly in the presence of several more or less distinct veins on the outer third of the membrane which are absent in other wasps. Sharov interprets these as the termini of branches of the radial sector and of media. Bradley (1921b), however, notes the presence of "accessory spurs" in this position in many Mutillidae, and suggests that in *Plumarius* these veins arose from such spurs.

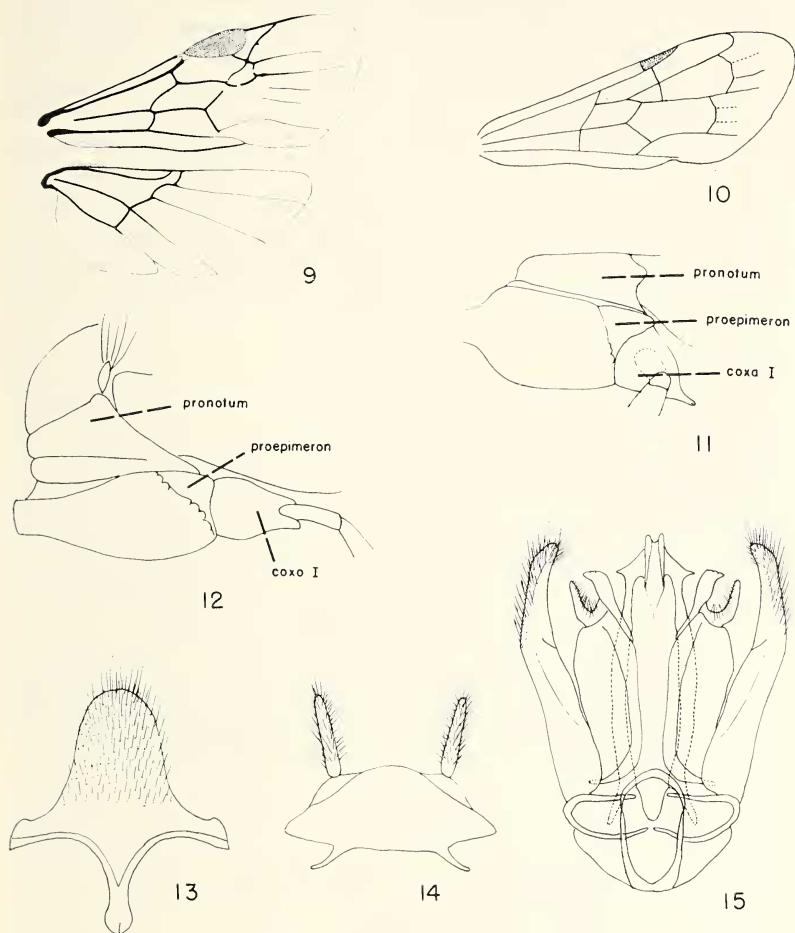


Fig. 9. Wings of male *Plumarius*. Fig. 10. Front wing of *Cretavus sibiricus* Sharov (Cretaceous) (after Sharov, 1957). Fig. 11. Lateral view of anterior part of thorax of female *Plumarius*. Fig. 12. Lateral view of anterior part of thorax of male *Plumarius*. Fig. 13. Subgenital plate (mesosomal sternite VIII) of male *Plumarius*. Fig. 14. Apical tergite (mesosomal tergite VIII) of male *Plumarius*, showing pygostyles. Fig. 15. Male genitalia.

I have described another group of wasps also having 13-segmented antennae in the female and sharing some features with the Scolioidea and some with the Bethyloidea. This is the family Scolebythidae (Evans, 1963), known from one genus and species in Madagascar and one genus and species in Brazil. Female scolebythids are winged and apparently adapted as parasites of wood-boring insects. I described the family without knowledge of the male, after considering and rejecting the possibility that *Plumarius* might represent the male sex of scolebythids. This was a fortunate decision, since I have not only discovered the female *Plumarius* but also a male of the scolebythid *Clystopenella longiventris* Kieffer. This male was with a series of females of this species collected by Fritz Plaumann on October 5, 1952, at Rondon, Paraná, Brazil. There is virtually no sexual dimorphism in this species, except that the male metasoma is simple, lacking the modification of sternite V of the female, and the terminalia are of course different (though the slide mount I made of the terminalia was lost before I studied it in detail, and I am therefore still unable to present any notes on the terminal structures of the male). Other minor differences from the female are as follows: antennae considerably more slender, though otherwise similar; vertex considerably less produced above the eye tops; front femora less robust. The structure of the mesosoma is especially similar in the two sexes, including all details of the wings.

There is no question, then, that the Scolebythidae and Plumariidae represent two very different families, now both known from both sexes. In the former there is little sexual dimorphism, and one assumes that both sexes are associated with burrows in wood in which their hosts live. In the Plumariidae there is marked sexual dimorphism, the females presumably searching for their hosts beneath the ground in deserts, the males flying about at night. Both families retain certain generalized features which suggest that they arose from a very primitive aculeate near the common ancestor of the Scolioidea and Bethyloidea: of special note are the 13-segmented antennae in both sexes, the fairly well defined proepimeron, and the lack of a constriction between the first two metasomal segments. The many striking differences are in large part associated with the very different habitats these wasps are believed to occupy. Probably the two families have evolved independently of each other and of other Aculeata since before the beginning of the Tertiary. A cladist would doubtless argue that both deserve superfamilial status. A realist might at the same time point to this as still another indication of the difficulties of grouping the Aculeata into superfamilies. As a realist,



I would go so far as to ask if (assuming the superfamily is a useful category in other Hymenoptera) all Aculeata ought not to be placed in a single superfamily.

Finally, a word should be said about *Plumarius* as a possible progenitor of the ants. Brown and Nutting (1950) point out that the venation of the male is in some ways antlike, although they remark that in general the male is "not a very promising candidate for ant ancestry". This remark seems even more applicable to the female, which has a very broad, smooth junction between the first two metasomal tergites, only five segments in the maxillary palpi, and a variety of unantlike specializations in body form. *Anthobosca*, in the Tiphidae, remains a much better prototype for the ants.

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